

Systematics, morphometrics and biogeography of the genus *Aubria* (Ranidae, Pyxicephalinae)

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New data are given on geographic distribution and morphometric variation with reference to geographic origin and sex in *Aubria subsigillata* (Duméril, 1856) and *Aubria masako* Ohler & Kazadi, 1990. The recently described *Aubria occidentalis* Perret, 1995 is here considered as a synonym of the former. Different statistical approaches are used to describe the taxa and the observed variations. A hypothesis of femoral gland function is formulated in the genera *Aubria* and *Pyxicephalus*. A phylogeny of the group *Aubria-Pyxicephalus* (Pyxicephalinae) is discussed.

INTRODUCTION

Naturalists conducting systematics and biogeographical surveys often encounter two patterns of distribution. A species can have a distribution-limited area, with little morphological variation, or a very wide distribution, within which one frequently observes significant variation that may lead to more than one interpretation. Often discrimination of distinct units is not discrete, and taxonomic decision difficult if collection localities are distant from each other. Even when we are conscious of variation problems in biology and use appropriate sampling methods, old samples generally include too few specimens for statistical comparison.

A recent study of frogs of the ranid genus *Aubria* (OHLER & KAZADI, 1990) led us to distinguish a new species (*Aubria masako*) from the central region of Zaire, North of the Congo. This species is clearly distinct from the type-specimen of *Rana subsigillata* from Gabon (DUMÉRIL, 1856). Specimens from 17 other localities of western Africa were referred to the species *Aubria subsigillata* by use of morphometrical (internarial distance, snout-nostril distance, diameter of tympanum) and morphological (presence of femoral glands, presence of mid-dorsal stripe) data. However, it was not possible to assign three frogs in the Paris Museum collection from the Sangha region, because they showed characters which distinguished them from our samples. The collection of further data was needed to resolve the question of their relationships.

Another problem presented by the literature was the presence of femoral glands in some of the frogs of populations without mid-dorsal stripes and their absence in others (DE

WITTE, 1930, PARKER, 1936; PERRET, 1966). PERRET (1966) had indicated that variation exists in this character among the frogs of Cameroon, and recently (1995) he discussed variation of this character in relation to sex. Finally, according to AMIET (personal communication), in Cameroon there are two different mating calls in *Aubria*, characterizing two kinds of frogs that are also distinct in distribution and ethology.

Recently, I collected important additional information on frogs of the genus *Aubria*. This gives a more detailed knowledge of the distribution of these frogs, contributes to the biogeography of Africa, and to the study of morphometrical variation in the taxa involved. Discussion of homology of femoral glands in this genus might give some interesting clues for use of these glands as characters in phylogenetic analysis.

In a recent paper, published after this work was completed and submitted, PERRET (1995) described a new species, *Aubria occidentalis*, from West Africa (type-locality in Ivory Coast). Its synonymy with *Aubria subsigillata* will be discussed under this species.

MATERIAL AND METHODS

ABBREVIATIONS

The names of the collections where the studied specimens are deposited are abbreviated as follows: BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; K, KAZADI Mpetemba collection; KMMA, Koeniglijk Museum voor Midden-Afrika, Tervuren; MHNG, Muséum d'Histoire naturelle de Genève; MNHN, Muséum national d'Histoire naturelle, Paris; MRHN, Institut Royal des Sciences naturelles de Belgique, Brussels; NMW, Naturhistorisches Museum, Wien; ZMB, Zoologisches Museum, Berlin; ZMH, Zoologisches Museum, Hamburg

For abbreviations of measurements, see Table I.

SPECIMENS STUDIED

For this study I measured 117 adult and juvenile frogs from 41 different collecting sites. Of these, samples from 31 sites contain adult specimens (a total of 65 individuals), including 21 localities with one specimen, 5 with two, 4 with three to eight and one locality with 15 adult specimens. As my data were collected over a five-year period, in the beginning the list of measurements was not exhaustive and consequently some individuals had to be excluded from statistical analysis.

COMPOSITION OF SAMPLES

The unit used for morphometrical analysis (sample) is a group of individuals of about the same age, of the same sex and of the same locality. For this purpose three age-groups

Table I. - List of abbreviations for measurements.

Abbreviations	Descriptions of measurements
EL	Eye length
EN	Distance from front of eye to nostril
FFTF	Distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe
FL	Femoral length (from sagittal axis of body to knee)
FLL	Fore limb length (from elbow to base of outer palmar tubercle)
FOL	Foot length (from base of inner metatarsal tubercle to tip of toe)
FTL	Fourth toe length (from base of proximal subarticular tubercle)
GD	Greatest diameter of femoral gland
GLDT	Distance of femoral gland to sagittal axis of body
HAL	Hand length (from base of outer palmar tubercle to tip of finger)
HL	Head length (from back of mandible to tip of snout)
HW	Head width
IBE	Distance between backs of eyes
IFE	Distance between fronts of eyes
IMT	Length of inner metatarsal tubercle
IN	Internarial distance
ITL	Inner toe length from distal edge of inner metatarsal tubercle
MBE	Distance from back of mandible to back of eye
MFE	Distance from back of mandible to front of eye
MN	Distance from back of mandible to nostril
MTFF	Distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe
MTTF	Distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe
NS	Distance from nostril to tip of snout
SVL	Snout-vent length
TFL	Third finger length (from base of proximal subarticular tubercle)
TFTF	Distance from maximum incurvation of web between third and fourth toe to tip of fourth toe
TL	Tibia length
TYD	Greatest tympanum diameter
TYE	Distance from tympanum to back of eye

were recognized: larvae, with a tail; juvenile frogs, from metamorphosis to sexual maturity; and adult frogs, including females with ripe ovaries and oviducts and males with well developed testes (DUBOIS, 1976). Secondary sexual characters are absent in adult *Aubria*, so it is difficult to determine adult males based on external and internal observation. But morphometrical analysis showed an important allometric difference between subadult and adult males that allows staging of the specimens. Subadult males, when analysed using the Laurent's technique (described below), cluster in a group of their own, independent of species membership, as do females (results not shown).

The best way to identify interpopulational variation is to treat the different samples separately. Only some samples have enough specimens for such comparisons. As sample sizes are usually too small for statistical analysis, I also grouped the frogs on a morphological basis, and compared the homogeneity of the two species.

In order to optimize analysis and to find an intermediate way between analysis of single population samples and species comparisons, I grouped specimens from populations of homogeneous biogeographic areas (WÜSTER & THORPE, 1992). The areas were defined following the studies of SCHIÖTZ (1967) and HAMILTON (1988) who have discussed possible biogeographic zones. The following areas were used (fig. 1): (1) Sassandra Valley, Ivory Coast; (2) Ghana; (3) Kovié, Togo, (4) Nigeria, West of Niger; (5) Nigeria, between Niger and Cross Rivers; (6) lowlands of Guinean Coast south of Cross River; (7) Sangha region at the intersect of Cameroon, Gabon and Zaire; (8) western part of Zaire; (9) eastern part of Zaire (this latter division is possibly due to a discontinuity in collecting).

MEASUREMENTS AND TRANSFORMATIONS

Measurements were taken with slide-calipers and binocular microscope. The precision varies from 0.1 % to 1 % of the measurement; for distances smaller than 3 mm, precision is only 1 % to 3 %.

Snout-vent length is given in millimetres. The other measurements are expressed as thousandths (‰) of snout-vent length:

$$RX = (X / SVL) \times 1000.$$

The position of the femoral gland on the thigh is expressed as the ratio of "femur" length (FL) to distance of gland from sagittal axis: FLGLDT = (FL / GLDT) × 1000. Webbing is given as the ratio (ITFOL) of webbing from the tip of the fourth toe to the incurvation between the third and fourth toe (TFTF) divided by the length of the foot (FOL), or as the ratio (MTFFOL) of webbing from the distal border of the metatarsal tubercle to the incurvation between the third and fourth toe (MTFF) divided by the length of the foot (FOL).

The logarithm of the measurement was used in discriminant analysis:

$$LX = \ln X.$$

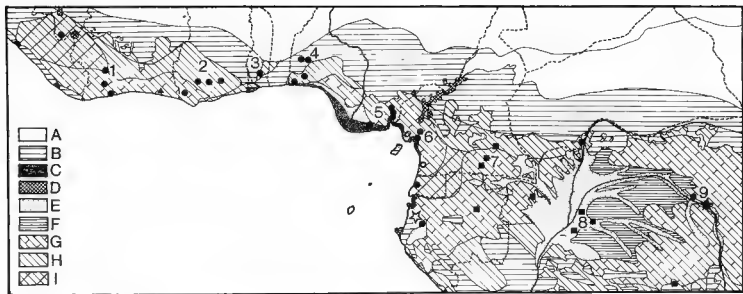


Fig. 1. — Distribution of *Aubria subsigillata* and *Aubria masako* in relation to vegetation types of tropical Africa. Black circle, *Aubria subsigillata*; white star, type-locality of *Rana subsigillata* A. Duméril, 1856; white circle, type-locality of *Phrynopsis ventrimaculata* Nieden, 1908; black triangle, type-locality of *Aubria occidentalis* Perret, 1995; black square, *Aubria masako*; black star, type-locality of *Aubria masako* Ohler & Kazadi, 1990. Forest types: A, Sudanian woodland; B, lowland rain forest; C, mangrove; D, Afromontane vegetation; E, swamp forest; F, mosaic of swamp forest and wetter lowland Guineo-Congolian rain forest; G, wetter lowland rain forest; H, drier Guineo-Congolian rain forest; I, mosaic of G and H. Biogeographical areas: 1, Ivory Coast; 2, Ghana; 3, Togo; 4, western Nigeria; 5, eastern Nigeria; 6, coastal area of Cameroon and equatorial Guinea; 7, Sangha region; 8, western Zaire basin; 9, eastern Zaire basin.

To calculate Laurent's distance, SVL was used as a size factor and all measurements were corrected as follows.

$$IX = [\ln X - \ln SVL].$$

All these corrections were used to standardize for isometric size changes.

STATISTICS

Mean, standard deviation, minimum and maximum were calculated for all variables of all groups on a personal computer using the SPSS program (NORUSIS, 1992). To estimate homogeneity, Haldane's coefficient of variation was calculated (DELAUGERRE & DUBOIS, 1985).

Non-parametric statistics permit comparison of samples of relatively small sizes (DUBOIS, 1984; DELAUGERRE & DUBOIS, 1985) and are therefore appropriate to use on samples from old zoological collections. Standard non-parametric statistics (ZAR, 1984) were applied to compare different populations. The Kruskal-Wallis test was used on all 35 measurements to measure group homogeneity. Those measurements which showed significant differences were subsequently treated by Tukey type B tests (on ranks of variables). The Mann-Whitney U test was used for comparison between any two groups.

LAURENT (1955, 1981) developed a method that uses distance measurements to compute phenograms. Cluster analysis using Laurent's procedure was made for adult males including the 35 measurements (for female frogs the sample size was too small to perform an analysis) on SPSS using Manhattan distance dissimilarities matrix and Ward's method (NORUSIS, 1992).

To investigate variables that distinguish the two morphologically recognized species, I performed a discriminant analysis. In the first analysis, all log-transformed measurements were included. In a further step, five variables with good discrimination characteristics (small in-group variation indicated by a relatively small Wilk's lambda) were retained to assign cases to their group based on a few measurements.

DESCRIPTIVE METHODS

The webbing formula of MYERS & DUELLMAN (1982) was used. Tadpoles were staged following GOSNER (1960). Keratodont formulae (DUBOIS, 1995) are given according to ANNANDALE'S (1912) system.

RESULTS

The genus *Aubria* is widely distributed in western and central Africa (fig. 1). Its distribution includes forested areas of the following countries: Guinea, Ivory Coast, Ghana, Togo, Nigeria, Cameroon, Congo, Republic of Central Africa, Zaire, Equatorial Guinea, Gabon. In life these are very colourful frogs with a typical yellow and violet

ventral pattern (PERRET, 1966: Cameroon; PERRET, 1995: West Africa; OHLER & KAZADI, 1989: Zaire; LAURENT, personal communication, letter of 22 June 1994: Zaire). The frogs of the different regions have a superficial resemblance – they were referred to one species from the description of *Rana subsigillata* in 1856 to 1990 – but detailed morphological studies show extensive interpopulational variation.

External morphology clearly separates the frogs into two groups: one with midfemoral glands and the other with close-to-knee femoral glands (see also PERRET, 1995). In a previous study (OHLER & KAZADI, 1990), because of an insufficient number of specimens, we did not realize the presence of near-to-knee femoral glands in *Aubria masako*. The character of gland position is correlated with dorsal colour and ontogenetical variation of ventral pattern.

The morphometrical homogeneity of morphologically determined groups was tested using the Kruskal-Wallis test. The test showed no significant differences at the $P = 0.05$ level for samples of adult males and females of *Aubria subsigillata* for the following measurements and ratios: SVL, RHW, RHL, RTL, RIN, RTYD, RTFL, LFGLDT, MTFOL. Male and female samples of *Aubria masako* were tested for the same measurements. Only the samples of males showed significant differences in the ratio RIN ($\chi^2 = 11.4$; DF = 5; $P = 0.04$ *).

COMPARISON OF SPECIES

Univariate comparisons

Interspecies comparisons were performed separately for males and females. The observed differences were the same as found in our previous study (OHLER & KAZADI, 1990), but treating the sexes separately underlines the differences observed. The morphometrical differences concern the head, the femoral gland position and the webbing.

Comparison of *Aubria subsigillata* and *Aubria masako* by means of Mann-Whitney U tests shows that there are statistically significant differences in both sexes in the ratios to SVL of several measurements (Table II). *Aubria subsigillata* is larger and has a longer tibia than *Aubria masako*. The webbing of its foot is more extensive. Differences exist between males and females in interspecific differentiation. In female *Aubria*, the Mann-Whitney U tests show no significant differences for several ratios concerning head (RHW, RHL, RTYD) and webbing (TFTFOL) that show significant differences in males.

Discriminant analysis

Using only five morphometric variables, adult specimens of *Aubria* can be attributed to one of the two species recognized (Table III). This permits also to classify the holotype of *Aubria occidentalis* in the *Aubria subsigillata* group. The variables are position and size of femoral gland, tibia length, metatarsal tubercle, distance between eyes and size of tympanum. They describe various aspects of the body form. Other variables were excluded because of missing values or of great variability of the measurements.

Table II. - Species differences between *Aubria subsigillata* and *Aubria masako*, all localities pooled, males and females treated separately. N, number; SD, standard deviation; V, coefficient of variation; U, Mann-Whitney U; P, probability; SUB, *A. subsigillata*; MAS, *A. masako*, for other abbreviations, see Table I and text.

Measurement	Species	N	Mean	SD	V	U	P
Males							
SVL	SUB	17	79.1	4.1	5.31	16.0	0.000***
	MAS	12	71.4	4.5	6.43		
RHW	SUB	17	349	11.63	3.37	40.0	0.006**
	MAS	12	363	16.3	4.58		
RHL	SUB	17	412	11.9	2.93	50.0	0.021*
	MAS	12	428	20.7	4.94		
RTL	SUB	17	388	14.1	3.68	30.0	0.001**
	MAS	12	368	16.0	4.26		
RIN	SUB	17	66	3.8	5.84	8.0	0.000***
	MAS	11	60	1.7	2.89		
RTYD	SUB	17	73	5.9	8.20	33.0	0.002**
	MAS	12	83	8.2	10.09		
LFGLDT	SUB	13	370	45.7	12.59	0.0	0.001***
	MAS	6	516	21.3	4.30		
RMETF	SUB	15	242	15.3	6.42	21.0	0.006**
	MAS	9	222	14.7	6.80		
TFTFOL	SUB	17	445	38.8	8.85	42.0	0.008**
	MAS	12	480	27.0	5.75		
Females							
SVL	SUB	17	86.0	4.1	4.84	28.0	0.004**
	MAS	10	78.4	6.0	7.84		
RHW	SUB	17	348	9.3	2.71	77.0	0.688 ns
	MAS	10	344	21.0	6.26		
RHL	SUB	17	403	13.9	3.50	68.0	0.393 ns
	MAS	10	399	16.1	4.14		
RTL	SUB	17	385	17.4	4.59	6.0	0.000***
	MAS	8	352	18.1	5.30		
RIN	SUB	16	66	4.3	6.62	13.0	0.001***
	MAS	9	58	3.6	6.38		
RTYD	SUB	17	74	5.7	7.81	47.0	0.056 ns
	MAS	10	79	7.0	9.08		
LFGLDT	SUB	13	334	55.8	17.03	0.0	0.000***
	MAS	8	487	53.4	11.31		
RMETF	SUB	15	230	18.8	8.31	3.0	0.003**
	MAS	5	196	9.72	5.21		
TFTFOL	SUB	16	450	37.5	8.46	61.0	0.317 ns
	MAS	10	456	28.0	6.29		

Table III.- Use of discriminant function to distinguish *Aubria subsigillata* and *Aubria masako* (adult males and females together) based on 5 morphometric parameters (see "Material and methods").

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	P
3.8584	0.8912	0.2058	68.76	5	0.0000

B. Standardized canonical discriminant function coefficients.

Morphometric character	Function 1
Tibia length	0.69064
Tympanum diameter	- 0.34850
Distance of femoral gland	- 0.45144
Diameter of femoral gland	- 0.38166
Distance between posterior part of eyes	0.60099

C. Classification success

Actual group	Predicted group	
	<i>Aubria subsigillata</i>	<i>Aubria masako</i>
<i>Aubria subsigillata</i>	30 (100%)	0
<i>Aubria masako</i>	0	15 (100%)
<i>Aubria occidentalis</i> holotype (ungrouped)	1	0

Laurent's morphometric distance

Measurements of males from all localities were included in LAURENT's (1955, 1981) procedure, which separated the two species very clearly (fig. 2). One group includes the type-specimens of *R. subsigillata* and *A. occidentalis* and corresponds to the morphologically determined *A. subsigillata*. The second group includes specimens from Masako, Boteke and Sangha and the type series of *A. masako*.

COMPARISON OF POPULATIONS

The inter-group differences that are significant at the $P < 0.05$ level obtained by the Tukey test are shown in fig. 3 for males and in fig. 4 for females.

In males, the differences between OTUs 2, 3, 4, 6 and OTUs 7, 8, 9 appear clearly. In females, where the number of specimens is very small even when the populations are grouped, the relations between the OTUs appear slightly different. The population 3 of *A. subsigillata* from Togo seems to be morphologically closest to *A. masako* populations 7, 8, 9. Comparison of the specimens from population 7 (Sangha region) with populations from western Zaire (8) and eastern Zaire (9) shows that they should be included in *A. masako*.

DETAILED ACCOUNT OF SPECIES

Aubria Boulenger, 1917

Aubria Boulenger, 1917: 988. — Type species by monotypy: *Rana subsigillata* Duméril, 1856

The types of *Aubria subsigillata* and of *Aubria masako* have been described in detail (DUMÉRIL, 1861: 224, pl. XVIII fig. 1, ÖHLER & KAZADI, 1990). Here I will give a description of the variation and of sexual dimorphism within populations, descriptions of tadpoles and young frogs, and diagnoses for the two species.

***Aubria subsigillata* (A. Duméril, 1856)**

Rana subsigillata A. Duméril, 1856: 560. — Holotype: MNHN 1566. — Type-locality Gabon.

[*Rana (Aubria) subsigillata*]: BOULENGER, 1917: 988.

Aubria subsigillata: LAURENT, 1953: 27.

Phrynosoma ventrimaculata Nieden, 1908: 499. — Holotype: ZMB 20134. — Type-locality: Longji, Cameroon. — Synonymy fide ÖHLER & KAZADI, 1990.

Aubria occidentalis Perret, 1995: 258. — Holotype: MHNG 2129.17. — Type-locality: Banco forest reserve, Ivory Coast. — New synonymy.

Specimens studied. — GABON. MNHN 1566, holotype of *Rana subsigillata* A. Duméril, 1856; Biligone River: MNHN 1974.1130; 50 km SW of Lambaréné. MNHN 1901.564. — EQUATORIAL GUINEA. Benito River: ZMH A.03133. — CAMEROON. Yabassi District (4°N, 10°E): BMNH 1938.6.10.9; SW-Province, "Korup": BMNH 1982.746; Yaoundé Road, 4

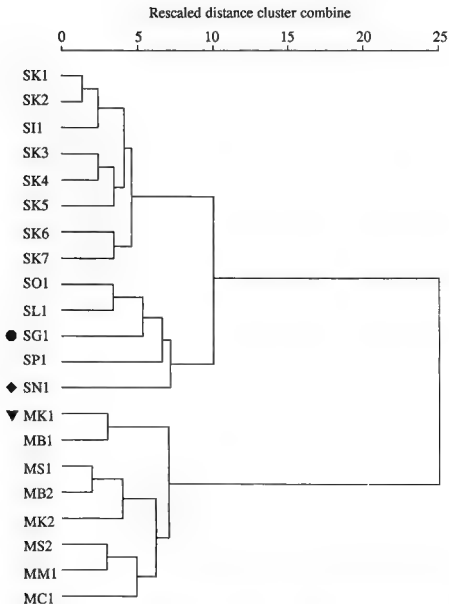


Fig. 2. — Phenogram of 21 adult males belonging to the species *Aubria subsigillata* and *Aubria masako*: Laurent's distances based on 35 measurements were included in distance calculations, using Ward's method. S, *A. subsigillata*: K, Kovié, Togo: 1, MNHN 1989.2054; 2, MNHN 1993 1462; 3, MNHN 1989.2056; 4, MNHN 1993.1966, 5, MNHN 1993 1469; 6, MNHN 1989.2050; 7, MNHN 1989.2053; I, Ibadan Swamp, Nigeria: 1, BMNH 1964.237; L, Lambarene, Gabon: 1, MNHN 1901 564; O, Obuasi, Ghana: 1, BMNH 1917.4.13.13; G, Gabon: 1, MNHN 1566, holotype of *R. subsigillata* (black circle), P, Port Harcourt, Nigeria: 1, BMNH 1956.1.10.84; N, Banco forest, Ivory Coast: 1, MHNG 2129.17, holotype of *A. occidentalis* (black square). M, *A. masako*: K, Kisangani, Zaire: 1, MNHN 1989.2775, holotype of *A. masako* (black triangle); 2, MNHN 1989.3305, paratype; B, Boteke, Zaire: 1, KMMA 85.30.B.368; 2, KMMA 85.30.B.362; S, Sangha, Congo: 1, MNHN 1993 2831; 2, MNHN 1989.2830, M, Mabali, Zaire: 1, CAS 145297; C, Coquilhatville, Zaire: 1, CAS 113967

ALYTES 13 (4)

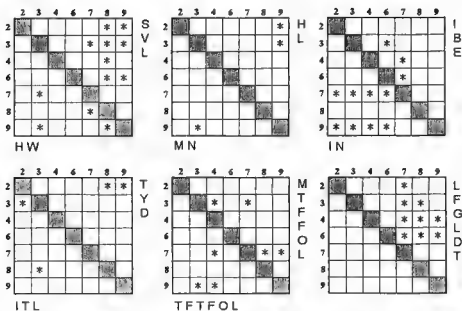


Fig. 3. — Significant differences (P < 0.05) of measurements among males of *Aubria*, grouped populations of biogeographically homogeneous areas, using the Mann-Whitney U test. 2, Ghana; 3, Togo; 4, western Nigeria; 6, coastal area of Cameroon and equatorial Guinea; 7, Sangha region; 8, western Zaire basin, 9, eastern Zaire basin. For key to measurement abbreviations see Table I.

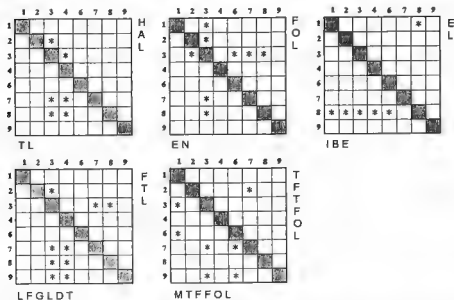


Fig. 4. Significant differences (P < 0.05) of measurements among females of *Aubria*, grouped populations of biogeographically homogeneous areas, using Mann-Whitney U test. 1, Ivory Coast; 2, Ghana; 3, Togo; 4, western Nigeria; 6, coastal area of Cameroon and equatorial Guinea; 7, Sangha region, 8, western Zaire basin, 9, eastern Zaire basin. For key to measurement abbreviations see Table I.

mi E of Douala: CAS 103804. – NIGERIA. NMW 2552; Calabar, Edge of Great Kwa River: BMNH 1980.1275; Calabar, 20 km north on MCC Road: BMNH 1980.1276; Calabar, 15 km north on MCC Road: BMNH 1980.1277; Ibadan: BMNH 1969.3000; Ibadan Swamp: BMNH 1964.237; Ijebu Ode: BMNH 1969.2999; Lagos: NMW 2555; Port Harcourt: BMNH 1956.1.10.84. – GHANA. Eastern Region, Tafo Cocoa Research Institute: CAS 146050-51, CAS 144214-215; Eastern Region, Kadé, Agricultural Research Station of University of Ghana: CAS 103783, CAS 103818, CAS 103836, CAS 104016, CAS 104051, CAS 125534; South Ashantee, Obuasi: BMNH 1917.4.13.12-13; Western Region, "Wasaw Akropong" (north of Tarkwa): CAS 97967. – TOGO. Kovié: MNHN 1989.2047-2056 and 1993.1463-1472; Mission Tové: MNHN 1989.4094. – GUINEA. Diéké: MNHN 1920.147. – IVORY COAST. Dalo-Lobo: MNHN 1993.929-930 (formerly A 929 and A.930); Sassandra: MNHN 1993.2832-2834; Soubre: MNHN 1989.4095; Banco forest reserve: MHNG 2129.17, holotype of *Aubria occidentalis* Perret, 1995.

Diagnostic characters. – *Aubria subsigillata* has femoral glands in a position midway from knee to vent in a ventral position on the thigh (fig. 5). The femoral gland is rounded. Feet are more webbed (I 1 – 2 II 1 – 2 III 1 – 2.5 IV 2.5 – 1 V) than in *Aubria masako*. Coloration of dorsum is uniform and structure of skin is smooth. Ventral mottled pattern tends to disappear in adult frogs on throat first.

Synonymy. – Direct comparison of the holotype of *Aubria occidentalis* Perret, 1995 with the holotype of *Rana subsigillata* A. Duméril, 1856 (see DUMÉRIL, 1861, pl. XVIII, fig. 1) and morphometric analysis (fig. 2) clearly indicates synonymy of the two names. This study includes also material from Ghana, included in the list of localities of paratypes of *A. occidentalis* by PERRET (1995). Another piece of evidence is given by the distribution of *Aubria occidentalis*, which coincides exactly with the distribution of *Aubria subsigillata*. PERRET (1995) did not examine material of both species from Gabon (see OHLER & KAZADI, 1990: 34, fig. 6, for the "mid-thigh gland" form of Gabon). In particular, he did not study the type specimen of *Rana subsigillata*. Morphological analysis does not show major differentiation within frogs of the genus *Aubria* from western Africa. Morphometric comparison of larger samples of *Aubria subsigillata* from Gabon with western populations and studies using other techniques (such as bioacoustics), might lead later to division of *A. subsigillata*. The name *Aubria occidentalis* Perret, 1995 would then be available for the western taxon.

Sexual dimorphism. – In the genus *Aubria*, no secondary sexual characters are known. Males lack vocal sacs, nuptial pads on fingers, and spinosities on different parts of the body. Thus sexes cannot be distinguished externally.

A sample (from Kovié, Togo) large enough to allow statistic comparison between males and females was studied. The most striking morphometrical difference between males and females is their size (Table IV). Females are significantly larger than males. Of the ratios to SVL of the 34 other measurements taken, only two show significant differences (Table IV). The eye is relatively longer in males than in females and the femoral gland is nearer to the base of the thigh (sagittal axis) in females than in males.



Fig. 5. - Position of femoral glands in females of *Aubria subsigillata* (above, MNHN 1993.1468, Kovié, Togo) and of *Aubria masako* (below, MNHN 1993.2830, Ivindo, Gabon). Ventral view of right thigh. Scale: 10 mm.

Morphological comparison shows that femoral glands are more developed in females than in males. These composite glands are structures that are prominent and more brightly colored and yellowish in females (fig. 6). In males the presence and position of the glands can be recognized primarily by colour.

Table IV. - Morphometrical differences between males and females of a population of *Aubria subsigillata* from Kovié, Togo. SD, standard deviation; MIN, minimum; MAX, maximum; U, Mann-Whitney U; P, probability.

Measurement		Mean	SD	MIN	MAX	U test
SVL	♂ n=8	77.83	4.70	67.2	83.4	U=0
	♀ n=7	86.44	2.60	83.6	89.7	P<0.001 ***
REL	♂ n=8	108.73	6.09	100.7	121.0	U=7.0
	♀ n=7	100.74	4.94	93.7	104.8	0.01 < P < 0.05 *
RGLDT	♂ n=8	159.70	13.64	140.1	183.0	U=7.0
	♀ n=7	130.55	22.33	95.3	164.6	0.01 < P < 0.05 *

Table V. - Measurements (in mm) on tadpoles of *Aubria masako* as compared to *Aubria subsigillata* from SCHIÖTZ (1964). SUB, *Aubria subsigillata*; MAS, *Aubria masako*.

	SUB	MAS (stage 37)	MAS (stage 40)
Total length	39	41.3	46.4
Snout-vent	16	18.8	19.0
Eye-eye	2.2	3.24	3.44
Nare-nare	2.0	1.55	1.75
Tail height	7.5	7.78	8.80
Keratodont formula	2:4+4/3	2:3+3/3	2:4+4/3

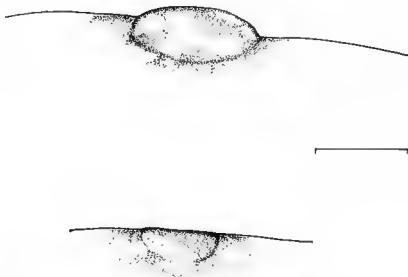


Fig. 6 - Sexual differentiation of femoral glands in *Aubria subsigillata* from Kovié, Togo. Above gland of left thigh of female (MNHN 1993.1468) and below gland of left thigh of male (MNHN 1993.1466). Scale: 5 mm

Larval characters. - A larva of this species was described by SCHIØTZ (1963) who gave drawings of a general view and of mouthparts. Larval keratodont rows formula: 2:4 + 4/3 (Table V). Body length: 16 mm; tail length: 23 mm.

Distribution. - The species occurs in western and central Africa to Gabon in the coastal area. The westernmost area of *Aubria subsigillata* is the valley of Sassandra river in Ivory Coast and Diéké in southern Guinea, near the Liberian border (fig. 1). Lambarene (Gabon, 0°41'S) is the most southern collecting point known.

***Aubria masako* Ohler & Kazadi, 1990**

Aubria masako Ohler & Kazadi, 1990: 29. - Holotype: MNHN 1989.2775. Type-locality: Masako forest, near Batibongena village, 15 km from centre of Kisangani on the ancient road to Buta, Zaire.

Specimens studied. - ZAIRE. Masako: MNHN 1989.2775, holotype; MNHN 1989.3305-3311, K 1049, K 1266, K 1324-1326, K 1463-1464, K 2505, K 2510-2511, K 2520, K 2528, K 2626, K 3500, K 3933; Boteke swamp: KMMA 85.21.B.123-141, KMMA 85.30.B.365-367; near Coquilhatville: CAS 113967-113968; Equateur Province, Bikoro Territory, Lotende Swamps near Mabali: CAS 145297; Sankuru Province, Lodja Territory, Omaniundu: CAS 145276; Yangambi: KMNH 15478. - GABON. Ivindo: MNHN

1993.2830-2831. — CONGO. Sangha: MNHN 1945.13, 1994.1665-1666. — REPUBLIC OF CENTRAL AFRICA. Zimba: MNHN 1993.4451. — CAMEROON. ZMH A 03134; Batouri District (4°N 14°25'E): BMNH 1934.12.1.2; Batouri District (3°75'N 13°75'E): BMNH 1937.1.1.1; Bitye: NMW 2554 (3 specimens), NMW 2557; Ya River (Dja): NMW 2553; Efa Yong (Efangono): NMW 2556.

Diagnostic characters. — The femoral glands are not in mid-femoral position, but closer to the knee (fig. 5) and in a more posterior position than in *Aubria subsigillata*. The femoral glands are more elongated and feet are less webbed (I 1½ — 2 II 1 — 2½ III 2 — 3 IV 2½ — I V) than in *Aubria subsigillata*. The dorsal pattern is clear with darker spots on slight warts. A mid-dorsal line may be present. In adults the ventral mottled pattern disappears on vent region, and remains more visible on throat.

Chresonymy. — Specimens from Ivindo forest (Gabon) listed under the name *Aubria subsigillata* by PERRET (1995) are morphologically similar to specimens from Zaire and should bear the name *Aubria masako*.

Adult morphology. — Before this study, this species was known only from the type-locality and neighbouring regions (OHLER & KAZADI, 1990). Morphological variation in this group is very important. In fact three specimens of the Sangha region of Cameroon, that could not be assigned clearly to one of the two species in 1990 due to fixation problems, are here tentatively placed in this group on the basis of femoral gland position, as well as other specimens from other localities, although some of them show major differences with the specimens from the type-locality. In the population from western Zaire (Boteke), that is different in many morphometrical characters (fig. 4), 4 specimens out of 20 (20 %) have a mid-dorsal stripe, a frequency lower than that observed in the type-locality (i.e. 65.2 %, N = 23) (OHLER & KAZADI, 1990).

Size at metamorphosis. — I was able to study a sample from Boteke (Zaire) composed of specimens of all three age-groups. This series includes numerous froglets in metamorphosis, exhibiting the specific characters already present, and two tadpoles with complete mouthparts.

The size just before metamorphosis (Gosner stage 45) varies from 18.3 to 20.0 mm (mean SVL = 19.37; N = 13; SD = 0.46).

After metamorphosis (mean SVL = 22.6 mm; extremes 22.1-23.2 mm; N = 3; SD = 0.55), the froglets already have femoral glands in the characteristic position. These three specimens are without mid-dorsal line and ventral pattern is complete (dark with whitish spots).

Larval characters. — Two tadpoles with complete mouthparts were studied (Table V; fig. 7). The younger tadpole (Gosner stage 37) is lighter in colour than the older tadpole (Gosner stage 41) and metamorphosing tadpoles. The vent and lateral parts of the body both already have the typical coloration of *Aubria*: dark with white spots. In general appearance it resembles the tadpole figured by SCHØTZ (1963). Measurements are very similar with the exception of internarial distance that seems to be smaller in *masako*

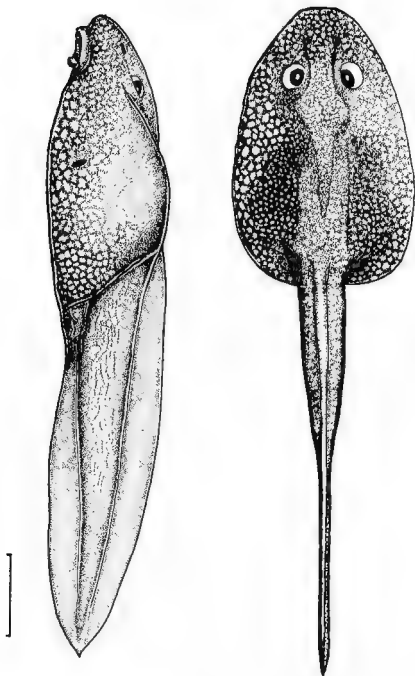


Fig. 7. — Tadpole of *Aubria masako* (KMMMA 85 21 B.141) from Botoko, Zaire (dorsal and lateral view, Gosner stage 37). Scale: 5 mm.

tadpole (51‰ of total length in the single tadpole of *subsigillata* and 38‰ in both tadpoles of *masako*) just as it is in adults (Table II). All characters, including the keratodont rows, must be studied on larger samples of tadpoles of both species.

DISCUSSION

SPECIES DIFFERENTIATION IN THE GENUS *AUBRIA*

Geographic morphological variation seems to be less important in *Aubria subsigillata* than in *Aubria masako*. In *A. subsigillata* morphology seems to be very similar over the wide range of distribution from Ivory Coast to Gabon despite important collection gaps. No major morphometrical differences were detected between samples of different geographic origins.

It seems doubtful that gene flow alone can explain this homogeneity. Some populations must have been separated for an extended period of time, however no major variations in morphology can be observed that would indicate heterogeneity in the underlying genotype. Such observation lends support to the hypothesis of the unity of the genotype (MAYR, 1975) due to molecular, genetic and evolutionary constraints.

In contrast, *A. masako* seems to be a more variable group with probably several subgroups, at least one in western central Africa (Gabon, Congo, western Zaire), and another one in eastern and central Zaire. These two subgroups might be interpreted as subspecies, but more detailed data on distribution and morphological variation of *Aubria masako* should clarify the situation.

PHYLOGENETIC CONSIDERATIONS

At present there is no general accepted classification of ranid frogs (DUELLMAN, 1975; FROST, 1985; LAURENT, 1986; FEI et al., 1990; DUBOIS, 1992; BLOMMERS-SCHLÖSSER, 1993; EMERSON & BERRIGAN, 1993), as the classification of Ranoidea is in a state of revolution. It did not change for almost a century. BOULENGER (1920) proposed to subdivide the genus *Rana* in several subgenera. This was followed in the African region by subsequent recognition of several genera. But the same did not occur in the other areas, particularly Asia, where members of this group show the most important radiation. Works on phylogeny and systematics of Asian ranids were published in Chinese (LU & HU, 1961; FEI et al., 1990) and ignored in Western countries. The work of CLARKE (1981) was a first step to analyse relationships of ranid subgroups and led DUBOIS to propose his 1987b classification. DUBOIS (1992) included many new data on morphology of ranid frogs. As the main problem remains the classification of the genus *Rana*, which is clearly polyphyletic, subdivision of this genus in provisional subgenera allows formulation of phylogenetic hypotheses more easily. Further work is needed to resolve the higher categories (tribes becoming subfamilies, subfamilies becoming families, etc.). This does not affect nomenclatural stability, because generic allocation of many species in *Rana* is

maintained. Nevertheless keeping of Dicroglossinae in the genus *Rana* is no longer possible, as members of the Dicroglossinae comprise a well identified monophyletic group (OHLER & DUBOIS, 1989; EMERSON & BERRIGAN, 1993). For these reasons, I here follow DUBOIS' (1992) classification. According to this classification, the genera *Aubria* and *Pyxicephalus*, which have long been known to be closely related (PROCTER, 1919), constitute together the subfamily Pyxicephalinae.

Femoral glands are present in phylogenetically distinct anuran groups. They can be found in Pelobatidae and in several families of Ranoidea. In the Mantellidae, Phrynobatrachidae and the ranid subfamily Ranixalinae, the glands are present in male specimens only or are much more conspicuous in males than in females. This suggests that these glands are not homologous to those present in the Pyxicephalinae, where the reverse is observed (see below). In fact such a puzzling distribution of this structure among anurans suggests a high level of homoplasy. For Pyxicephalinae the presence of femoral glands can be interpreted as an apomorphic character supporting the monophyly of the group.

Three important characters allow distinction of the two species of *Aubria* (see also PERRET, 1995): the position of the femoral gland, the mid-dorsal line and the ventral pattern. Only the position of the femoral glands is constant in all post-metamorphic specimens of a given species. In some old alcohol preserved specimens that were dried and had their colour changed to blackish, the femoral glands are hard to recognize.

The position of the glands is either mid-femoral or close-to-knee. No ontogenetic changes were observed. In specimens (males and females) of the genus *Pyxicephalus*, femoral glands are found in the close-to-knee position (FLGLDT = 534; SD = 84.5; N = 23) as in *A. masako*. No variation in gland position has been found in this genus (SUEUR & OHLER, in preparation). This position of femoral glands is therefore interpreted here as the plesiomorphic character state. The mid-thigh position of femoral glands present in *A. subsigillata* is here interpreted as the apomorphic character state.

The mid-dorsal line is a feature observed in two of the 40 populations studied; both have femoral glands in close-to-knee position. In other frog species, the presence-absence of a mid-dorsal line has been shown to be determined by a single gene (MORIWAKI, 1953; DUBOIS, 1979; BERGER & SMIELOWSKI, 1982). This coloration pattern can be found in *Pyxicephalus* and in the Dicroglossinae, the possible sister-group of the Pyxicephalinae (CLARKE, 1981; DUBOIS, 1987b, 1992). In the populations of *A. subsigillata*, a mid-dorsal line was never observed. The permanent absence of the mid-dorsal line, here viewed as a secondary loss of an allele from the gene pool of the species, is the apomorphic character state. The possible presence of mid-dorsal line is the plesiomorphic state of this character.

The third character is the ventral colour pattern. Three different states can be distinguished and form an ordinated transformation (0 → 1 → 2). The absence of ventral coloration pattern can be found in Dicroglossinae and in *Pyxicephalus* and is the plesiomorphic state (0). The intermediate state is the presence of a ventral pattern of whitish rounded patches on a dark ground in young ontogenetic stages (older larvae and juvenile frogs) and the gradually disappearing in adult stage (1). This is observed in *Aubria masako*. In the third state, the colour pattern remains distinct in adults (2). I interpret this as a partial pedomorphism sensu DUBOIS (1987a): a somatic feature (here, ventral colour pattern) shows juvenile character in an adult phenotype. This state is present in *Aubria subsigillata*.

The subfamily Dicroglossinae, represented by the genera *Hoplobatrachus* (species *occipitalis* and *tigerinus*) and *Conraua*, is defined by CLARKE (1981) by one character: 7,1 P – anteriorly reduced preorbital process of pars fascialis of the maxilla.

The Pyxicephalinae (*Pyxicephalus* and *Aubria*) are a monophyletic group defined by CLARKE (1981) by 5 apomorphic characters: 2,1 – presence of cranial exostosis, 4,1 P – presence of occipital canal; 6,1 – a zygomatic ramus of the squamosal much longer than the otic ramus and articulating with the postorbital process of the pars fascialis of the maxilla, 14,3 – strong overlap of the anterior border of parasphenoid ala by the medial ramus of the pterygoid articulating along at least 1/2 the anterior width of the parasphenoid ala; 19,1 – sternal style a long bony element tapering markedly anteriorly to posteriorly.

The genus *Pyxicephalus* is defined by three apomorphic characters: 9,1 – pterygoid process of maxilla well developed, directed postero-medially, overlapping anterior ramus of pterygoid, with which it forms a suture, 16,1 P – base of the omosternum slightly forked, the greatest space between the arms being less than half the width of one arm; 22,4 – terminal phalanges of fingers and toes reduced, almost cone-like.

Superposition of the new characters defined above on the cladogram proposed by CLARKE (1981) (fig. 8) corroborates the phylogeny of CLARKE (1981), and one apomorphic character of *Aubria* has been defined.

BIOGEOGRAPHY

Aubria is generally considered as a genus limited to high forests (LAMOTTE, 1966, SCHIÖTZ, 1967). Comparing our locality data with vegetation maps (WHITE, 1983) seems to agree with these statements. Nevertheless, one must be very careful with this kind of data, because geographical maps may not reflect the detailed local situation. In many regions, forest is very sparse and fragmented due to human activities. When precise collection data are available for *Aubria*, they mention forest localities or forest border areas. Distribution of the two species is in fact closely related to rain forest distribution in Africa.

African tropical forest is not a homogeneous ecosystem. Several forest types can be recognized (WHITE, 1983). Several biogeographic refuges or core areas can be recognized from distribution data of vertebrates (HAMILTON, 1988). Two major refugia areas can be found on the western and eastern border of the Zaire basin. Two biologically somewhat more impoverished areas can be found in western Africa in Sierra Leone and Liberia, and in eastern Ivory coast and western Ghana. The Zaire basin seems to be an area of disjunct distribution for many taxa. The distribution gap corresponds to the area of the swamp forest (WHITE, 1983). *Aubria* seems to be absent from this swamp forest; this could be due to the presence in this forest of an open canopy which resembles secondary forest, where *Aubria* seems to be absent (SCHIÖTZ, 1967).

However, AMIET (1989) included *Aubria* among the species occurring in modified forest habitats. He found choruses in secondary habitats, in forest swamp areas or even

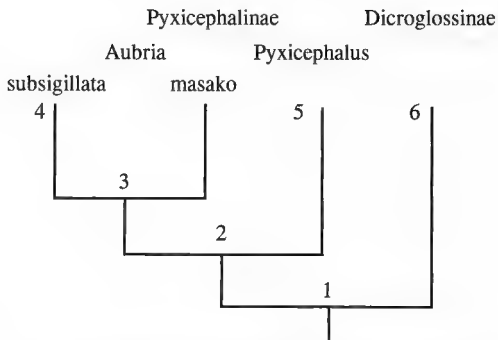


Fig. 8. — Interrelationships of Pyxicephalinae as proposed by CLARKE (1981). The tree was rooted with Dicroglossinae (genus *Hoplobatrachus*) as the outgroup. Nodes 1, 2 (in part), 5 and 6 have been defined by CLARKE. Node 2 is corroborated by one additional synapomorphy discussed in the present study (femoral glands present in both sexes close to knee position). Nodes 3 and 4 are each supported by an apomorphic state of the transformation series of the ventral pattern coloration (node 3: ventral colour pattern in juvenile stages; node 4: ventral colour pattern also in adult stage). Node 4 is further supported by an additional apomorphy (permanent absence of mid-dorsal line).

in open swamp areas (AMIET, personal communication). Further exploration of central African forest should clarify the ecological preferences of the two species of *Aubria*.

Two species of *Aubria* are present in the central African forest area. From geographic distribution, *Aubria subsigillata* appears to be a form distributed in lowland rain forest near the west and central African coast. *Aubria masako* is found in the basin of the Congo river and in the Cameroonian plateaus. In Cameroon and Gabon, where the two species occur, the distinction of a coastal form (*subsigillata*) and a "continental" form (*masako*) is clear (PERRET, 1995, as *occidentalis* and *subsigillata* respectively).

The character analysis indicates an eastern Zaire basin origin for *Aubria*. Starting from the Zaire basin, *Aubria* has colonized the entire area of tropical forest of central and western Africa. Splitting up of the forest in historical dry periods might be a factor of the evolution of two species. The observed intraspecific variation might result from ecological isolation. Further investigations using call analysis and adequate samples for morphometrical studies might discriminate further taxa.

FUNCTION OF FEMORAL GLANDS

The femoral glands, either in mid-femoral or close-to-knee position, are always present, in males, females and juveniles examined (smallest specimen in metamorphosis, KMMA 85.21.B.125: SVL = 18.3 mm). Their observation is sometimes difficult due to fixation problems. Often a small incision of the skin in the presumed gland region can resolve the doubt: if a gland is present, the skin shows a basal thickening due to the large size of glandular cells.

The difference in position of the femoral glands is distinctive but not sufficiently significant to question gland homology. The correlation of a large set of characters between the two species and to their outgroup *Pyxicephalus* confirms this homology.

Nothing is known of the biological signification of this gland. In a large sample of *Aubria subsigillata* (23 specimens from Kovié, Togo), the development of the gland (prominence) seems to depend on the sex of the frogs. Adult females have clearly more prominent glands than males whose glands can be recognized only by their different colour (fig. 6). This is confirmed by PERRET's (1995) observation on samples from Ivory Coast (under the name *A. occidentalis*). Nevertheless in other specimens it is still difficult to distinguish male and female specimens on external characters only. In further investigations attention should be paid to seasonal variation of femoral gland size, development and colour in *Aubria*.

In Mantellidae and Phrynobatrachidae, femoral gland aggregates are visible or more developed in males. As femoral glands, and other ventrally positioned glands, of males are in contact with females during amplexus, a stimulatory function of femoral gland secretions is assumed (DUELLMAN & TRUEB, 1985: 58).

In *Aubria*, schooling of tadpoles has been observed (SCHIÖTZ, 1963). A similar behaviour is known in *Pyxicephalus adspersus*, another species of the subfamily Pyxicephalinae (POYNTON, 1964: 95). Tadpoles are "very gregarious" and tend to swarm around the male of *Pyxicephalus* remaining in the water. Even juveniles have been known to form swarms (POYNTON, 1964). It would be interesting to understand the nature of these aggregations.

Tadpoles of various species recognize their siblings and distinguish tadpoles of different clutches. This behaviour has been particularly studied in the American toad *Bufo americanus* (WALDMAN, 1985). Factors that allow sibling recognition seem to be fixed or modified in ontogenetic development. A factor permitting sibling recognition might be transferred between the sibling tadpoles, or it might be transferred from the mother to her offspring. Differential recognition of maternal half-siblings by separately reared tadpoles suggests contribution of a factor of the maternal parent (product of oviduct for example) (WALDMAN, 1981). The secretion of female femoral glands might be such a primary factor for *Aubria* and *Pyxicephalus* offsprings. It would provide a basis for learning the sibling smell chemical characteristics. This gland secretion might be deposited by the mother on the eggs while laying them and gland function might be determined by the ovulatory hormone system. This hypothesis is more congruent with having active glands in females than the traditional hypothesis of stimulatory function during amplexus. Another kind of

"sexual character reversal" in anurans is known in *Limnodynastes peroni* (Myobatrachidae, Limnodynastinae), where females bear lateral fringes on the fingers (DUELLMAN & TRUEB, 1985: 56-57): in this species, females use their hand in paddling movements for stirring water and spawn into a foam nest. The use of a secondary sexual character in offspring care would be an interesting parallelism. Experimental investigations could be carried out on *Aubria* and *Pyxicephalus* to test the hypothesis of chemical transmission of family recognition.

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